Water Transfer from Soil to Seed: The Role of Vapor Transport

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ABSTRACT

Mixed solid-water-gas media such as soil can supply water to a dry object as both liquid and vapor. Modelers and agricultural engineers have commonly assumed liquid transport dominates imbibition by seed. This study tests the hypothesis that vapor is the major source of water for imbibition under normal soil moisture conditions. Water uptake was measured under varying degrees of seed-soil contact. Wheat (*Triticum aestivum* L.) seeds were suspended in holes in blocks of moist soil (average water potential −0.16 MPa). Hole diameter varied from 13 to 0 mm (no hole), so that the distance between the moist soil and the seed varied from a maximum of 5 mm to intimate seed-soil contact. The amount of water absorbed by seed in 24 h increased from 15 to 17 mg seed^{-1} as seed-soil contact increased from none to maximum contact, indicating that at least 85% of the water absorbed by seed in intimate seed-soil contact could be attributed to vapor alone. Reevaluation of the role of vapor transport should result in improved multiphase transport models in soil and other media.

It has been generally assumed that a seed surrounded by a moist solid-liquid-gas media such as soil will imbibe water mostly as liquid through contact with water films coating the solid particles. In the validation of seed imbibition and germination models, however, data have often failed to demonstrate sensitivity to different hydraulic conductivity rates through soils at various water potentials (Hadas and Russo, 1974; Collins et al., 1984; Lafond and Fowler, 1989). Models which add water vapor transport (Rogers and Dubetz, 1980; Bouaziz and Bruckler, 1989) may have underestimated diffusive vapor flux over short distances. At soil water potentials from field capacity down to −1.0 MPa, the soil atmosphere will be above 99% relative humidity (Papendick and Campbell, 1981). Compared with liquid flux, vapor flux would, therefore, be little influenced by normal variations in soil water potential. If water vapor plays a much greater role in imbibition than previously thought, it would explain the insensitivity of models based on hydraulic conductivity.

Wuest et al. (1999) demonstrated that wheat seed separated from soil by a layer of fiberglass cloth germinate as quickly as seed in intimate seed-soil contact. Some have pointed out, however, that the fiberglass may not have been free of microscopic water films, or that condensation may have played a role in the fiberglass treatment and not when seed was surrounded by soil. Also, that experiment measured germination, which involves a combination of imbibition and time-dependent seed physiology. The objective of this study was to measure imbibition of water by wheat seeds that had different degrees of seed-soil contact. My hypothesis is that most of the water imbibed by seeds can be supplied as vapor, and therefore it should not be assumed that liquid flow through seed-soil contact is the dominant source.

MATERIALS AND METHODS

The experimental apparatus consisted of a hand-packed block of soil 16 cm wide by 7 cm long by 5 cm high (Fig. 1). The soil block had 3-cm deep holes ranging in diameter from 2 to 13 mm. Individual wheat seed glued to plastic dowels were suspended in the holes. Two of the ten seed positions had no hole and were designated as zero diameter. Epoxy adhesive glued the non-embryo end of wheat seed to 3-mm diam. plastic dowels. The plastic dowels were inserted into 3-mm holes in the soil box lid, so that when the lid was lowered into place the seed would be suspended at a 2-cm depth in the soil holes. The wheat seed was 3 to 3.5 mm in diameter, so holes of 9 to 13 mm resulted in the seed being suspended without touching soil. In smaller holes the seed would occasionally or partially contact soil. In the smallest holes, the seed pressed tightly against the sides of the holes. In the two positions with no hole, the seed was forced straight down 2 cm into the soil.

The soil was a Walla Walla silt loam (coarse-silty, mixed, mesic Typic Haploxeroll; 18% clay, 70% silt, and 12% fine and very fine sand). Two grams powdered blue dye (Brilliant Blue FCF, C.I. Food Blue 2; C.I. 42090; N-Ethyl-N-{4-[(4-{ethyl[(3-sulfophenyl) methyl]amino}phenyl)(2-sulfophenyl) methylene]-2,5-cyclohexadien-1-ylidene}-3-sulfobenzene-methanaminium hydroxide inner salt, disodium salt; $C_{37}H_{34}N_2Na_2O_9$-S_3) per kilogram of soil was added to detect seed-soil contact. The soil was sieved through a 4-mm sieve, moistened, mixed, and allowed to equilibrate several weeks in a closed container. Soil moisture was determined gravimetrically after each run. Three separate batches of soil were used, and the soil water content was allowed to vary from run to run. Soil water content averaged 0.16 g water g^{-1} dry soil, and ranged from 0.10 to 0.21 g g^{-1}. This Walla Walla soil has a water potential of −1.1 MPa at 0.10 g g^{-1} and −0.06 MPa at 21 g g^{-1}. Soil water is presented here as calculated water potentials based on a water release curve (Wuest et al., 1999). The moist soil was packed to approximately 1 m^3 m^{-3} in 1-cm layers around dowels corresponding to the different hole sizes. The dowels were then removed, leaving clean well-shaped holes 3 cm deep in the 5-cm deep soil block.

Each seed-plus-stick assembly was dried at 105°C and weighed before being suspended in the soil block for 24 h at 25 ± 3°C. The sticks were then removed, soil quickly brushed off, and the seed and stick placed in a weigh jar and weighed again. The seed surface was visually rated for approximate dye coverage (rated as 0, 2.5, 25, 50, 75, or 100%).

A total of 42 runs were made. Two different randomizations of the hole size location in the soil block were used. There was no indication of any interaction between hole location and results. One run was performed without seeds to determine how much water the plastic dowels and glue absorb. Absorption by plastic dowels without seeds was consistent among hole sizes and amounted to <4% of the average absorption with seed. It was ignored in the data analysis.

The water gain data was fit to a two phase (two straight

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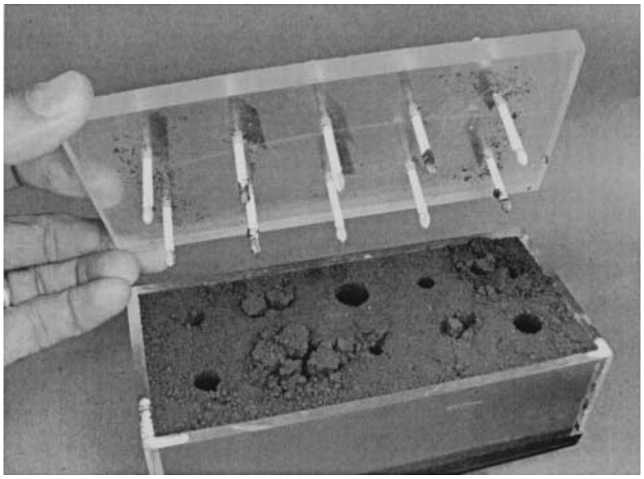

Fig. 1. Apparatus used to produce different amounts of seed-soil distance. Two of the ten seed positions had no hole, resulting in the seed being pressed directly into the soil. Wheat seed was glued to the plastic dowel.

lines) regression model (Draper and Smith, 1981). Fieller's theorem (Zerbe, 1978) was used to estimate the join point, where the lines intersect.

The seed was dried at high temperature (105°C) to ensure uniform starting water content and also to reduce the potential for respiration and germination to affect the ending weights. To make sure that drying at 105°C did not affect the seed's capacity to imbibe water, two runs using identical soil water content compared oven-dried and normal, air-dried seed. After 24 h the average water gain across hole sizes was the same for oven dried and normal seed (12.7 mg). Another comparison, using hole sizes of 0 and 11 mm, sampled at 4, 8, 16, 24, and 32 h, again demonstrated no differences in water absorption patterns over time and resulted in an average water gain of 9.6 mg for oven-dried and 9.3 mg for normal seed. Germination tests revealed that oven drying did increase time to germination from about 1 to 3 d.

To compare the equilibrium water content of seed in 0- and 11-mm diam. holes, 64-h runs were made using oven-dried seed. Each seed was weighed before being attached to a stick to allow calculation of water gain as a proportion of beginning dry weight. There were three replicate seeds for each time and treatment. Finally, germination of normal (not oven-dried) seed was compared between 0- and 11-mm holes at 30, 40, and 55 h. This run also used individually weighed seed, five replicates for each time and treatment.

RESULTS

No significant dye stains appeared on seed in holes greater than 7-mm diam. (Fig. 2). Average dye coverage increased from 0 to nearly 100% as hole size decreased from 7 to 2 mm. Seeds placed directly into soil without holes (0-mm holes) had the most dye coverage. Water gain by seeds in 24 h was 15 mg in the three largest holes, and increased to 17 mg with no hole (Fig. 2). The four runs with the driest soil, averaging −1.3 MPa, demonstrated very little, if any, influence of soil contact on water gain. In contrast, the five runs with the highest soil water potential, averaging −0.07 MPa, demonstrated an influence of soil contact on water gain which was slightly greater than the overall average.

When followed over a 64-h period, seeds in large

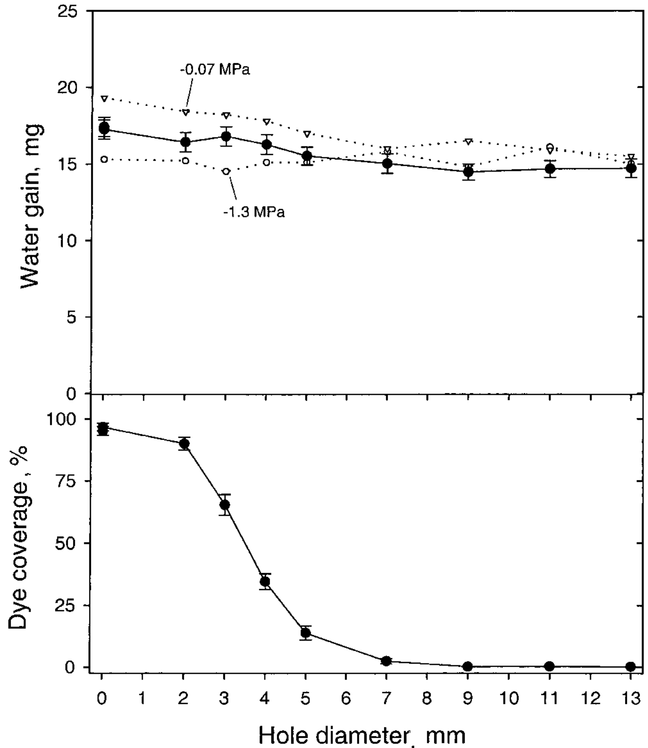

Fig. 2. Water gain and dye coverage of wheat seed suspended in holes of different diameter for 24 h. Error bars, where large enough to be seen, show standard error of the mean (n = 42). There were two zero diameter (no hole) positions in each soil block. Dotted lines indicate averages for the five runs with the greatest soil water potential (−0.07 MPa) and for the four driest (−1.3 MPa). Average soil water potential for all 42 runs was −0.16 MPa.

holes lagged behind in water gain compared with those with seed-soil contact (Fig. 3). The water gain difference averages 18%, which is similar to the 15% difference in water gain shown in Fig. 2. Soil water potential was −0.15 MPa, which is close to the overall average of the 42 runs (−0.16 MPa) shown in Fig. 2.

The germination test used seeds which were not oven dried at a high temperature (Fig. 3). At 40 h, seeds with soil contact were 100% germinated, whereas seeds in 11-mm holes were only 40% germinated. At 55 h all seeds were 100% germinated. The soil water potential for this germination test was moderate (−0.36 MPa). The jump in water gain at 55 h by seed with soil contact can be attributed to root growth. These seeds had been germinated for at least 15 h and had an average radicle length of 7 mm.

DISCUSSION

Seed-soil contact is difficult to estimate. Collis-George and Hector (1966) made theoretical calculations based upon simplified shapes and assumption of equilibrium between soil water and seed. Their wetted area estimate was 13.2% for closely packed 0.125-mm particles around a seed at equilibrium with −0.05 MPa water potential (a very moist soil). Therefore, even in a closely packed, moist soil, about 90% of a seed's surface is exposed to soil atmosphere. This soil atmosphere is at

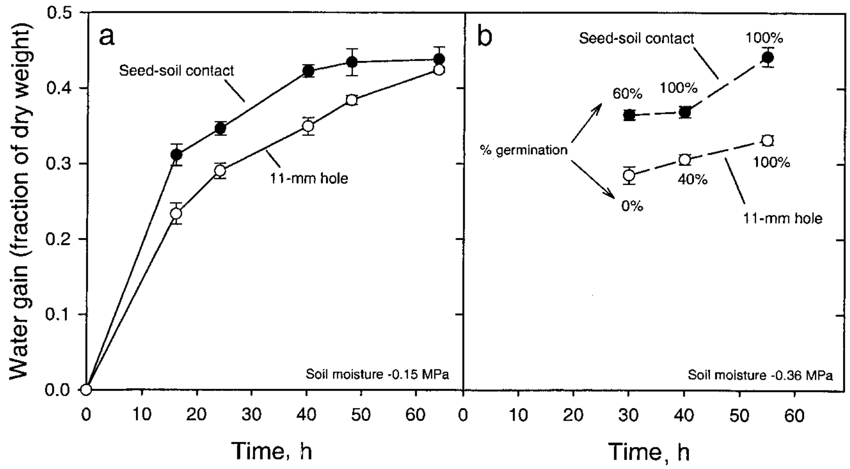

Fig. 3. Comparison of water gain and germination for wheat seed in good seed-soil contact and for seed suspended in 11-mm holes. Individual seed weights were used to calculate water gain on a dry weight basis. (a) Oven-dried (105°C) seed. At 64 h, water gain was 18.1 mg for soil contact and 17.5 mg for 11-mm holes. (b) Normal seed. The large increase in water gain at 55 h by seeds in soil contact is probably due to root growth, averaging 7 mm. Error bars, where large enough to be seen, show standard error of the mean: (a) $n = 3$, (b) $n = 5$.

nearly 100% relative humidity down to a water potential of −1.0 MPa.

Dry seed can absorb water rapidly in the form of vapor, as demonstrated in Fig. 2. In 24 h, seed supplied with vapor alone absorbed only 15% less water than seed in intimate soil contact. Soil water potentials from −0.07 to −1.3 MPa had no effect on the amount of water gained by seed without soil contact. If 85% or more of the water imbibed by seed can be supplied by vapor, it would greatly reduce the effects of water potential and seed-soil contact area.

It took 48 h to reach an equilibrium water content with seed-soil contact, and 64 h when seed was suspended in 11-mm holes (Fig. 3). Full germination occurred in 40 h with seed-soil contact and 55 h without. This proves that vapor alone is sufficient to supply water for imbibition and germination, and delays may be relatively small. In a previous study, an average delay in germination of only 5.6% was measured between seed in good seed-soil contact and seed separated from soil by a layer of fiberglass cloth (Wuest et al., 1999).

In the present study, the germination comparisons were between seed with very good soil contact and those with a seed-to-soil distance of about 4 mm (a 3-mm seed in an 11-mm hole). In the absence of convection, diffusion is slow except at very short distances (Denny, 1993). When attempting to measure imbibition of vapor by seed, researchers should not assume that a sealed vessel with water in the bottom maintains uniform humidity throughout the vessel, especially when dry seeds are present. Without significant convection, a gradient will develop between the water surface and the surface of the seed, which will slow imbibition of water (Collis-George and Melville, 1978). In the past, researchers estimating vapor flux to seed at distances of 1 or 2 mm (Bruckler, 1983; Owen, 1952) have concluded that vapor flux is more significant than researchers estimating vapor flux over distances of 10 mm or more (Schneider and Renault, 1997; Collis-George and Melville, 1978). A typical sown seed may have an average seed-to-water-film distance that is a fraction of 1 mm.

No increase in water gain was detected as hole diameter decreased from 13 mm to where soil contact started (Fig. 2). The water gain data can be fit to a two-phase model (Draper and Smith, 1981), with hole diameters $<$9 mm fit to a line with intercept 0.017 g and slope of -0.00034 g mm^{-1} (highly significant). Hole diameters 9 mm and greater fit a line with a slope not significantly different than zero. The two-phase regression model shows no evidence of significant lack of fit compared with an analysis of variance with hole diameter fit as a discrete effect. Applying Fieller's theorem (Zerbe, 1978) results in a join point for the two lines of 8.7 mm, with a 95% confidence interval of 5.2 to 11.1 mm. As indicated by dye coverage, seed-to-soil distances $<$3 mm (holes smaller than 9 mm) was confounded with increases in seed-soil contact. This experiment, therefore, did not provide evidence for an increase in vapor flux with decreasing seed-to-soil distance.

Does this experiment prove that vapor is the major source for imbibition when seed-soil contact exists? Where water films contact the seed, liquid transfer will occur. Unless the soil is very moist and very closely packed around the seed, however, most of the seed surface will be exposed to the same conditions as if no seed-soil contact existed. Unless the total water absorption rate is limited by the seed, vapor and liquid imbibition could occur simultaneously in proportion to the seed surface area affected by each. The area of seed surface actually in contact with soil particles would appear to be small under normal field conditions, when the soil is dry enough to operate seeding equipment.

The exact relative contributions of vapor and liquid to imbibition by seed with soil contact would be difficult to measure. However, the conclusions of this and other studies (Rogers and Dubetz, 1980, Livingston and de Jong, 1990; Wuest et al., 1999) indicate vapor should be regarded as the primary source of water for imbibition at normal soil moistures.

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